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Does the urban gradient influence the composition and ectoparasite load of nests of an urban bird species?

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Abstract: Urbanisation has profound impacts on birds via, for example, changes in activity budgets, distributions and movements influenced by resource availability, and the connectedness of preferred habitats. We live in an urbanising world and yet understand little about how urbanisation affects the basic biology of organisms that share urban spaces with us. A case in point is nest construction and nest maintenance behaviours that require significant investments of time and energy by birds early in the breeding attempt. Here, we studied how position on an urban gradient in the city of Birmingham, UK, influenced the composition and ectoparasite load of nests of Blue Tits (*Cyanistes caeruleus*). In total, we deconstructed 131 nests removed from nestboxes at the end of the breeding season in 2014 at 30 different locations along an urban gradient. Nest composition varied significantly along this gradient with significant relationships between feather content and built cover (negative), and connected tree cover (positive). Notably, anthropogenic materials were found in 73% of nests but their inclusion was unrelated to position on the urban gradient. The only identifiable ectoparasites in nests were Siphonapterans (fleas) and although ectoparasite load was unrelated to position on the urban gradient, it was positively related to nest mass. Taken together, we show that even for a common species that is often referred to as an 'urban adapter', the urban gradient influences nest composition and ectoparasite load, and thus potentially reproductive outcomes of small passerines. The challenge is to roll out this approach over multiple years to test the applicability of our findings over longer timeframes and their broader implications for a wide range of bird species that are routinely found breeding in increasingly urbanised landscapes globally.

1. INTRODUCTION

We live in a rapidly urbanising world (United Nations, Department of Economic and Social Affairs, Population Division, 2014) with 54% of the human population residing in urban areas in 2014. As a

result of urbanisation, many bird species have to adapt rapidly to the concomitant changes in habitat structure (Rodewald *et al.*, 2013), predation risk (López-Flores *et al.*, 2009), food availability (Jones and Reynolds, 2008), temperature regimes (Deeming *et al.*, 2012) and nest site availability (Chace and Walsh, 2006). In recent years there have been a number of studies that have documented marked changes in life-history strategies of birds co-existing with large (and ever increasing) human populations (reviewed in Chace and Walsh, 2006). For example, Chamberlain *et al*. (2009) found that when compared to non-urban birds, urban Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*) laid earlier, produced smaller clutches, reared lighter nestlings and had lower productivity per nesting attempt. These effects were mediated through widespread availability of supplementary food in urban areas resulting in birds in higher body condition laying eggs earlier than rural conspecifics (Schoech and Bowman, 2001); lower availability of natural foods, however, resulted in poorer provisioning of urban broods and thus ultimately reduced productivity. In another study Rolshausen *et al*. (2009) described a migratory divide between sympatric Eurasian Blackcaps (*Sylvia atricapilla*) that showed rapid changes in phenotype and reproductive isolation. This migratory divide was established through increased anthropogenic food availability in urban centres, resulting in changes in overwintering strategies of some birds and representing a possible mechanism for speciation.

We know much about how urbanisation influences the behaviour and ecology of birds with research findings summarised in a number of books (e.g. Bird *et al.*, 1996; Marzluff *et al.*, 2001; Lepczyk and Warren, 2012; Gil and Brumm, 2013). Fuller *et al*. (2012) found that the availability of food resources to birds breeding in urban areas was positively related to human population density both at regional scales and within a single large city (i.e. Sheffield, UK). The population densities of some small passerines such as the House Sparrow (*Passer domesticus*), the Common Blackbird (*Turdus merula*) and the Common Starling (*Sturnus vulgaris*) were positively related to the density of bird feeders in the city of Sheffield, UK. By contrast, other species that regularly visit bird feeders in urban gardens, such as Great and Blue Tits, Common Wood Pigeons (*Columba palumbus*) and Winter Wrens (*Troglodytes troglodytes*), they were not (Fuller *et al*., 2012).

Compared with our knowledge of how urbanisation influences bird distribution and abundance, our understanding of the nesting biology of birds in our towns and cities remains more limited (reviewed in Deeming and Reynolds, 2015). This is surprising given that investment of time and energy in nest building and maintenance is far from trivial in many species (Hansell, 2000; Stanley, 2002). Bird abundance is in part determined by their productivity but we now need to go beyond studies that, for example, simply examine how the breeding performance of birds varies with urbanisation (e.g. Tremblay *et al.*, 2003; Hedblom and Söderström, 2012; Partecke *et al.*, 2012). There is a pressing need to investigate nest building and resultant nest composition in response to urbanisation to allow us to understand in greater detail how such reproductive phases are shaped by ecological context and how they explain life-history strategies of birds. Smith *et al*. (2013) examined

how food availability (as a proxy for urbanisation) influenced nest building of Blue and Great Tits and found that food supplementation advanced the onset of nest construction and egg laying in both species, and truncated the nest construction period of Blue Tits (but not Great Tits). However, the nest-lining period was not influenced by food availability in either species. Nest composition has been examined in relation to altitude (e.g. Kern and van Riper, 1984), latitude (e.g. Deeming *et al.*, 2012; Mainwaring *et al.*, 2012), timing of laying (e.g. Mainwaring and Hartley, 2008; Britt and Deeming, 2011), and ectoparasite load (e.g. Petit *et al.*, 2002; Suárez-Rodríguez *et al.*, 2012), but not within an urban context. In the case of nest defence against ectoparasites, we know that many species actively select specific nest constituents to reduce the ectoparasite burden that if uncontrolled can dramatically reduce offspring growth and/or survival (reviewed in López-Rull and Macías Garcia, 2015).

In this study we examine how the composition and ectoparasite load of nests of an urban 'adapter' common passerine species, the Blue Tit (Croci *et al.*, 2008), varied along an urban gradient in the city of Birmingham, UK. First, we collected nests at the end of the 2014 breeding season from clusters of identical nestboxes at various points along an urban gradient (as defined by two land cover metrics) and deconstructed them to examine nest composition. Secondly, the same nests were examined to quantify ectoparasite load. In this way it was possible to examine how nest composition was related to the ectoparasite load experienced by the nest occupants.

2. METHODS

In January of 2014, 10 nestboxes were erected at each of 31 separate sites in the city of Birmingham that provided a broad range of diversity along two urban gradients defined according to connected tree cover and built cover. Descriptions of how the urban land cover measures were derived and a list of the 31 sites identified in the study are provided in Appendix 1. Figure 1 shows the distribution of some of these 31 sites throughout the city and representative photographs illustrate the habitat at each of them.

At the end of the breeding season (i.e. August 2014) all nests (N = 163) were removed from nestboxes and immediately placed in individual tin-foil containers with cardboard lids. Nests were then stored in a domestic chest freezer (Space Max Whirlpool, Whirlpool UK Appliances Ltd, Croydon, UK) prior to nest deconstruction. Nestboxes at one site (namely 'Grand Union Canal' – see Appendix 1 for further details) contained no Blue Tit nests and so subsequent findings are based on nests from the remaining 30 sites. All but three nestboxes, containing Great Tits, provided nests made by Blue Tits. Of these 160 nests, 107 progressed beyond the egg stage.

Each nest was removed from the chest freezer, any eggs and dead chicks still contained in the nest cup were removed and then it was weighed to the nearest 0.0001 g on an electronic balance (Sartorius 1712, Göttingen, Germany). Each nest was then defrosted overnight at room temperature for a minimum of 15 hours before processing. On average it took 1 hour and 34 minutes to process each nest in the laboratory by deconstructing them and assessing ectoparasite load. Each nest was then

separated into cup and base components by one person (AW) to maintain consistency and each was then weighed separately.

The cup and the base of each nest were deconstructed separately. Nest constituents were separated using fine-point tweezers and placed into the following categories: moss, dry grass, feathers, hair, fur, natural fibres and anthropogenic materials. Natural fibres consisted predominantly of wool or wool-like material while anthropogenic materials were fibres that had undergone processing such as plastics, dyed wool, cotton, *etc*.. Material of each constituent was weighed separately to the nearest 0.0001 g on an electronic balance (see above for details) and then stored in separate sealed Ziploc bags. The remaining material following separation of other nest constituents was weighed and then examined to quantify ectoparasite load of each nest. It comprised dead skin (from nestlings and tending adults), faeces, dust particles, invertebrates, pupae cases and any other nest material not falling into the main nest constituents. It was searched methodically twice using fine-point tweezers and a ×10 hand lens for all ectoparasites which were removed and counted into weighing boats. Following ectoparasite removal, all remaining material was stored in a sealed Ziploc bag. Subsequent identification of larvae removed from nest materials as being ectoparasites proved inconclusive and thus they were excluded from subsequent statistical analysis.

Statistical analysis of nest composition data treated the nest constituents separately but in the case of ectoparasite load, we combined hair, fur and natural fibres into a new category called 'animal fibres'; these nest materials are functionally alike in acting in a similar manner as substrate for ectoparasites in nests (Hansell, 2000). All statistical analysis was carried out using SPSS (SPSS 23 for Windows 7, IBM Corporation, New York, New York, USA). The sampling unit for analyses was the nest site location and thus all data from analyses of nest composition and ectoparasite load are presented as site averages (range: 1-9 nestboxes). This approach attempts to control for statistical non-independence of nests from the same site where habitat and microclimatic variables were likely shared across all nestboxes. However, summary data for nest mass and nest composition in terms of masses of the different are provided in Appendix 2.

Nests were categorised along the urban gradient into 'low' (0-33%), 'medium' (34-66%) and 'high' (67-100%) connected tree cover and built cover. This inevitably resulted in unequal sample sizes between categories for statistical comparisons. Proportional (bound) data were not normally distributed and thus were normalised using arcsine square-root transformation prior to one-way analyses of variance (ANOVA). Significant ANOVA outputs were followed by *post hoc* Tukey's tests. Ectoparasite loads were count data, were not normally distributed and so we used Mann-Whitney *U*-tests and Kruskal-Wallis tests for statistical comparisons. Linear regression analysis was used to elucidate relationships between variables where one could be established as a dependent variable. In all cases statistical analyses were conducted using an alpha threshold of 0.05.

3. RESULTS

148 In total 131 Blue Tit nests were deconstructed with 107 of them having contained live chicks during
149 the breeding season and 24 of them having failed at the egg stage.
150
151 **3.1 Nest composition**
152 All nests were composed of a base of moss with the nest lining comprising dry grass, feathers, natural
153 fibres, anthropogenic materials and fur (Appendix 2). The composition of nests according to the
154 relative masses of each of these components did not differ significantly in nests from low, medium
155 and high connected tree cover categories of the urban gradient (Fig. 2a; $F_{2,27} = 0.15$, $P = 0.86$).
156 However, the composition of nests from low, medium and high built cover categories of the urban
157 gradient was significantly different (Fig. 2b; $F_{2,27} = 5.70$, $P = 0.009$) with more natural fibres found in
158 nests in high built cover ($P < 0.05$).
159 If urban land cover is treated as a continuous (rather than a categorical) variable, few
160 statistically significant changes in nest composition were found along the urban gradient. Feathers
161 were the only nest component to be significantly positively correlated with connected tree cover (Fig.
162 3a; $R = 0.41$, $df = 28$, $P = 0.02$), and they were negatively correlated with built cover (Fig. 3b; $R = -$
163 0.42, $df = 28$, $P = 0.02$). Natural fibre content of nests was marginally negatively correlated with
164 connected tree cover (Fig. 3c; $R = -0.33$, $df = 28$, $P = 0.07$), but it was marginally positively
165 correlated with built cover (Fig. 3d; $R = 0.32$, $df = 28$, $P = 0.08$). Although anthropogenic materials
166 were found in 73% of all nests, their contribution to overall nest composition did not differ
167 significantly in relation to the location of nest sites along the urban gradient.
168
169 **3.2 Ectoparasite load**
170 Fleas (Siphonaptera) were the only ectoparasites discovered in the nests and on average each of the
171 131 nests that were deconstructed contained 184 fleas. The 107 nests that contained live pulli during
172 the 2014 breeding season contained many more fleas than the 24 nests that did not ($U = 380$, $n_1 = 107$,
173 $n_2 = 24$, $P < 0.0001$). As a result all subsequent analyses were performed on nests that only contained
174 pulli. Flea counts did not differ significantly in nests from low, medium and high connected tree cover
175 categories of the urban gradient ($H = 0.93$, $df = 2$, $P = 0.63$), and nor did they differ between built
176 cover categories of the urban gradient ($H = 0.77$, $df = 2$, $P = 0.68$).
177 Flea count did not appear to be dependent on the relative proportions of the different
178 components of nests (all R^2s < 0.07, all Ps > 0.05). The only nest trait that was related to flea
179 abundance was nest mass, with the two variables being positively related (Fig. 4; $R^2 = 0.27$, $df = 28$, P
180 $= 0.004$).
181
182 **4. DISCUSSION**
183 Compared with other reproductive phases, the nest phase (including its construction and ongoing
184 maintenance) is under-studied, especially in relation to the urban gradient. Therefore, our study was

185 based upon the general reproductive behaviour of small passerines in urban environments in response
186 to habitat connectivity, foraging resource and activity budgets, rather than on the specifics of their
187 nesting biology *per se*. Thus, we might have expected that birds in urban areas would construct nests
188 of similar insulative property to those constructed by birds in more rural areas providing benefits to
189 the former as a result of the urban heat island (UHI) effect translating into a warmer nest
190 microclimate. Alternatively, we might have expected that birds nesting in more urban environments
191 would have less well insulated nests because of the nest microclimate being warmer (Deviche and
192 Davies, 2014). However, both expectations are accompanied by the caveat that there is little evidence
193 to suggest that increases of even a few °C in ambient temperature associated with the UHI effect
194 influence the recrudescence of reproductive systems of birds and thus nest building, timing of egg
195 laying *etc.*. We also expected that in nests from more urban areas, the proportion of anthropogenic
196 materials might increase while that of more natural nest components might decrease, simply based
197 upon predicted changes in their relative availabilities along the gradient. Similarly, we also suspected
198 that Blue Tit nests might incorporate less natural aromatic plants (based upon their availability) at
199 more urban nest sites and thus that ectoparasite loads of such nests might increase (Mennerat *et al*.,
200 2009). However, with the study of Mennerat *et al*. (2009) having taken place in Corsica, we know
201 little about the presence of aromatic plants along our urban gradient and, if available, the propensity
202 of birds in the city to use them as nest constituents.
203 We found similar nest components to other studies of Blue Tit nests here in the UK and in
204 western mainland Europe (see Table 4.1 in Deeming and Mainwaring, 2015) with the exception that
205 nests at some sites such as RSPB Woodland – Cannon Hill Park and Soho Pool Wharf contained large
206 amounts of anthropogenic materials (see Appendix 2 for further details). Nevertheless, we found few
207 statistically significant effects of the urban gradient on the composition (Figs 2 and 3) and ectoparasite
208 loads (Fig. 4) of nests. The feather content of nests varied significantly in relation to connected tree
209 cover (positive) and built cover (negative), perhaps reflecting the availability of feathers to nest-
210 building birds. In Blue Tits we know that feathers are an important nest component (Britt and
211 Deeming, 2011) but Mainwaring *et al*. (2015) found that they may serve a signalling function in the
212 detection of intrusions by competitive birds into nestboxes of resident males, rather than providing a
213 thermoregulatory benefit during incubation and/or chick rearing as has been found in other species
214 (Møller, 1984). Nests of conspecifics either in artificial nestboxes or in natural tree cavities represent
215 sources of feathers to intruding birds that can be incorporated into their own nest contents. We would
216 predict that breeding density of tits is probably higher in areas of the city with less built cover
217 (reviewed by Marzluff, 2001), and more connected tree cover, but we lack such empirical data
218 currently from the city of Birmingham to investigate this hypothesis further. Further studies along the
219 urban gradient in the city might include assessments of: the usage of breeding sites other than
220 nestboxes we provided by tits in urban areas; the availability of natural and anthropogenic nest

materials at breeding sites; and how breeding density across the gradient influences the composition and ectoparasite load of individual nests.

We found that the relationships between natural fibre content of nests, and urban built cover and connected tree cover, were only marginally significant and our findings suggest that we need more data from more cities and over more breeding seasons before we can reach firmer conclusions. We understand very little about how far birds will travel to obtain such natural nest components in urban habitats but if they travel as extensively as they do in searching for micronutrients such as calcium in the pre-laying phase (*e.g.* Wilkin *et al*., 2009), then birds might cross many breeding territories of conspecifics and heterospecifics, risking many agonistic encounters, and flying many hundreds of metres, also risking elevated predation risk, in doing so. Given that Wilkin *et al*. (2009) examined birds breeding in a woodland outside of a city, further initial work is needed to study search efforts of birds nest building in cities and their investment in sourcing nest materials.

A surprise finding of the study was the presence of anthropogenic material (e.g. plastics, dyed wool, cotton) in most nests (73% of all nest deconstructed) irrespective of their position on the urban gradient. We had predicted that birds in areas with more built cover and less connected tree cover would have more ready access to such nest material. The inclusion of such materials in the majority of deconstructed nests suggests that birds may obtain significant benefits from them which may contribute to reducing energetic costs of incubating adults (Cresswell *et al*., 2003), and increasing chick growth rates (Lombardo *et al*., 1994), and ultimately fitness (Hepp *et al*., 2015). Surgey *et al*. (2012) provided artificially dyed wool of different colours to four tit species (Paridae) nesting in rural woodland and found that while the collection of it (as examined by nest deconstruction) appeared opportunistic, some birds travelled extensively to many different sources to collect it as valuable nest material. It is clear that we still know relatively little about the relative contributions of different nest constituents to breeding performance of birds in urban habitats. Until we know more, it is difficult to understand how such nest materials shape life-history strategies of urban birds.

Finally, we examined the relationship between the ectoparasite load of nests that had contained chicks during the breeding season and their position on the urban gradient; the only ectoparasites found were fleas. We know that nestboxes are more prone to infestations of fleas than natural cavities (Wesołowski and Stańska, 2001), but we were surprised that other nest ectoparasites (reviewed by López-Rull and Macías Garcia, 2015) were not detected during nest deconstruction. We found no indication that nesting Blue Tits had employed plant aromatics (Mennerat *et al*., 2009), cigarette butts (Suárez-Rodríguez *et al*., 2012) *etc.*. as defence against ectoparasites. Of course, extensive further work is required in the city to assess the availability of both to nesting birds across the gradient. Furthermore, there was no significant relationship between ectoparasite load and feather content of nests as we might have expected. Winkler (1993) found that removal of feathers from the nests of Tree Swallows (*Tachycineta bicolor*) depressed the growth of nestlings and resulted in them carrying greater ectoparasite burdens than nestlings in unmanipulated nests. The only significant

relationship was between ectoparasite load and overall nest mass (Fig. 4). To fleas and other ectoparasites in nests, those containing chicks represent the peak of food availability provided by brooding adults, growing chicks, faeces and undigested food in the nest lining (Heeb *et al*., 1996; Lea and Klandorf, 2002). Despite the criticisms of Wesołowski and Stańska (2001) of nestboxes and their inherent biases in studies such as ours, newly established nestboxes contained no material prior to the 2014 breeding season and thus ectoparasites counted in our study were associated with the current breeding attempt. Therefore, they had not burrowed into materials from previous seasons in order to enter diapause (Tauber *et al*., 1986).

There is an urgent need for further research to investigate the nesting biology of birds in urban habitats. Specifically, we need to know how changes in the built cover and connected tree cover brought about by land clearance and construction of roads and buildings, for example, influence the breeding performance of birds. Cavity nesters such as Blue Tits are an ideal study species in this regard but we acknowledge the concerns of Wesołowski (2011) who outlined reasons why nestbox studies are not directly comparable to those of birds nesting in natural cavities. Some of his recommendations, such as the reporting of type and size of nestboxes, are easily adopted, but others, such as comparisons with 'reference' natural cavities and assessment of avian breeding densities, are less easily derived in an urban environment for a species that breeds in such a diversity of nesting locations (Gosler and Clement, 2007). However, we accept the shortcomings of nestbox studies and we support the recommendations of Wesołowski (2011) that every effort should be made to provide as much accompanying information as possible in published outputs. Of course, the Blue Tit is a good model species for the study of city-dwelling birds but we continue to question how findings from our study can be applied to other 'urban' species. We believe that research over the next few years will significantly improve our understanding of the breeding biology of a number of such species and we encourage others in other large cities to respond to the challenge of working along their respective urban gradients. A pressing concern is how we quantify urbanisation within a relevant context for a breeding bird. Here, we assessed the urban matrix according to built cover and connected tree cover to identify potential sites for nestboxes but this still fails to control for considerable habitat heterogeneity between sites (Chamberlain *et al*., 2008). This is especially pertinent at the urban-suburban interface where dramatic changes in reproductive outputs in response to habitat type can occur (e.g. Crick *et al*., 2002). Recent developments using GIS by Seress *et al*. (2014) have shown some potential to relate urbanisation 'scores' directly to aspects of avian biology (i.e. body condition scores of House Sparrows [*Passer domesticus*]). Whether this approach offers similar benefits in assessing how urbanisation influences the nesting biology of birds remains to be tested but we hope that this, and other points of discussion in the present study, will urge researchers to investigate nest construction and maintenance in much more detail in the future.

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References

Bird, D.M., Varland, D.E. and Negro, J.J. (1996) *Raptors in human landscapes: Adaptation to built and cultivated environments*. Academic Press, London, UK.

Britt, J. and Deeming, D.C. (2011) First-egg date and air temperature affect nest construction in Blue Tits *Cyanistes caeruleus*, but not in Great Tits *Parus major*. *Bird Study*, **58**, 78–89.

Chace, J.F. and Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landsc. Urban Plan.*, **74**, 46–69.

Chamberlain, D.E., Cannon, A.R., Toms, M.P., Leech, D.I., Hatchwell, B.J. and Gaston, K.J. (2009) Avian productivity in urban landscapes: a review and meta-analysis. *Ibis*, **151**, 1–18.

Cresswell, W., Holt, S., Reid, J.M., Whitfield, D.P. and Mellanby, R.J. (1993) Do energetic demands constrain incubation scheduling in a biparental species? *Behav. Ecol.*, **14**, 97–102.

Crick, H.Q.P., Robinson, R.A., Appleton, G.F., Clark, N.A. and Rickard, A.D. (2002) *Investigation into the causes of the decline of Starlings and House Sparrows in Great Britain*. British Trust for Ornithology, Thetford, UK.

Croci, S., Butet, A. and Clergeau, P. (2008) Does urbanization filter birds on the basis of their biological traits? *Condor*, **110**, 223–240.

Deeming, D.C. and Mainwaring, M.C. (2015) Functional properties of nests. Pp. 29–49. In: Deeming, D.C. and Reynolds, S.J. (Eds). *Nests, eggs, & incubation: New ideas about avian reproduction.* Oxford Univ. Press, Oxford, UK.

Deeming, D.C., Mainwaring, M.C., Hartley, I.R. and Reynolds, S.J. (2012) Local temperature and not latitude determines the design of Blue Tit and Great Tit nests. *Avian Biol. Res.*, **5**, 203–208.

Deeming, D.C. and Reynolds, S.J. (2015) *Nests, eggs, & incubation: New ideas about avian reproduction*. Oxford Univ. Press, Oxford, UK.

Deviche, P. and Davies, S. (2014) Reproductive phenology of urban birds: environmental cues and mechanisms. Pp. 98–115. In: Gil, D. and Brumm, H. (Eds). *Avian urban ecology: Behavioural and physiological adaptations*. Oxford Univ. Press, Oxford, UK.

Fuller, R.A., Irvine, K.N., Davies, Z.G., Armsworth, P.R. and Gaston, K.J. (2012) Interactions between people and birds in urban landscapes. Pp. 249–266. In: Lepczyk, C.A. and Warren, P.S. (Eds). *Urban bird ecology and conservation*. Studies in Avian Biology No. 45, Univ. California Press, Berkeley, CA, USA.

Gil, D. and Brumm, H. (2013) *Avian urban ecology: Behavioural and physiological adaptations*. Oxford Univ. Press, Oxford, UK.

Gosler, A.G. and Clement, P. (2007) Family Paridae (Tits and chickadees). Pp. 662–750. In: del Hoyo, J., Elliott, A. and Christie, D.A. (Eds). *Handbook of the birds of the world*. Volume 12. Picathartes to tits and chickadees. Lynx Edicions, Barcelona, Spain.

Hale, J.D., Davies, G., Fairbrass, A.J., Matthews, T.J., Rogers, C.D.F. and Sadler, J.P. (2013) Mapping lightscapes: spatial patterning of artificial lighting in an urban landscape. *PLoS ONE*, **8**(5), e61460.

Hansell, M. (2000) *Bird nests and construction behaviour*. Cambridge Univ. Press, Cambridge, UK.

Hedblom, M. and Söderström, B. (2012) Effects of urban matrix on reproductive performance of Great Tit (*Parus major*) in urban woodlands. *Urban Ecosyst.*, **15**, 167–180.

Heeb, P., Werner, I., Richner, H. and Kölliker, M. (1996) Horizontal transmission and reproductive rates of hen fleas in great tit nests. *J. Anim. Ecol.*, **65**, 474–484.

Hepp, G.R., DuRant, S.E. and Hopkins, W.A. (2015) Influence of incubation temperature on offspring phenotype and fitness in birds. Pp. 171–178. In: Deeming, D.C. and Reynolds, S.J. (Eds). *Nests, eggs, & incubation: New ideas in avian reproduction*. Oxford Univ. Press, Oxford, UK.

Jones, D.N. and Reynolds, S.J. (2008) Feeding birds in our towns and cities: a global research opportunity? *J. Avian Biol.*, **39**, 265–271.

Kern, M.D. and van Riper III, C. (1984) Altitudinal variations in nests of the Hawaiian honeycreeper *Hemignathus virens virens*. *Condor*, **92**, 761–767.

Lea, R.W. and Klandorf, H. (2002) The brood patch. Pp. 100–118. In: Deeming, D.C. (Ed.). *Avian incubation: Behaviour, environment, and evolution*. Oxford Univ. Press, Oxford, UK.

Lepczyk, C.A. and Warren, P.S. (2012) *Urban bird ecology and conservation*. Studies in Avian Biology No. 45, Univ. California Press, Berkeley, CA, USA.

Lombardo, M.P., Bosman, R.M., Faro, C.A., Houtteman, S.J. and Kluisza, T.S. (1995) Effect of feathers as nest insulation on incubation behavior and reproductive performance of Tree Swallows (*Tachycineta bicolor*). *Auk*, **112**, 973–981.

López-Flores, V., MacGregor-Fors, I. and Schondube, J. E. (2009) Artificial nest predation along a Neotropical urban gradient. *Landscape Urban Plan.*, **92**, 90–95.

López-Rull, I. and Macías Garcia, C. (2015) Control of invertebrate occupants of nests. Pp. 82–96. In: Deeming, D.C. and Reynolds, S.J. (Eds). *Nests, eggs, & incubation: New ideas in avian reproduction*. Oxford Univ. Press, Oxford, UK.

Mainwaring, M.C. and Hartley, I.R. (2008) Seasonal adjustments in nest cup lining in Blue Tits *Cyanistes caeruleus*. *Ardea*, **96**, 278–282.

Mainwaring, M.C., Hartley, I.R., Bearhop, S., Brulez, K., du Feu, C.R., Murphey, G., Plummer, K.E., Webber, S.L., Reynolds, S.J. and Deeming, D.C. (2012) Latitudinal variation in blue tit and great tit next characteristics indicates environmental adjustment. *J. Biogeogr.*, **39**, 1669–1677.

Mainwaring, M.C., Wolfenden, A., Read, J.E., Robson, J.M.A., Tomlinson, C.J. and Hartley, I.R. (2015) Feathering the nest: the effects of feather supplementation to Blue Tit nests. *Avian Biol. Res*.

Marzluff, J.M. (2001) Worldwide urbanization and its effects on birds. Pp. 19–47. In: Marzluff, J.M., Bowman, R. and Donnelly, R. (Eds). *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA, USA.

Marzluff, J.M., Bowman, R. and Donnelly, R. (2001) *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA, USA.

Mennerat, A., Perret, P., Bourgault, P., Blondel, J., Gimenez, O., Thomas, D.W., Heeb, P. and Lambrechts, M.M. (2009) Aromatic plants in nests of blue tits: positive effects on nestlings. *Anim. Behav.*, **77**, 569–574.

Møller, A.P. (1984) On the use of feathers in birds' nests: predictions and tests. *Ornis Scand.*, **15**, 38–42.

Partecke, J., Van't Hof, T. and Gwinner, E. (2004) Difference in the timing of reproduction between urban and forest European Blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proc. R. Soc. Lond. B*, **271**, 1995–2001.

Petit, C., Hossaert-McKay, M., Perret, P., Blondel, J. and Lambrechts, M.M. (2002) Blue tits use selected plants and olfaction to maintain an aromatic environment for nestlings. *Ecol. Lett.*, **5**, 585–589.

Rodewald, A.D., Kearns, L.J. and Shustack, D.P. (2013) Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests. *Biol. Cons.*, **160**, 32–39.

Rolshausen, G., Segelbacher, G., Hobson, K.A. and Schaefer, H.M. (2009) Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. *Curr. Biol.*, **19**, 2097–2101.

Schoech, S.J. and Bowman, R. (2001) Variation in the timing of breeding between suburban and wildland Florida Scrub-Jays: Do physiologic measures reflect different environments? Pp. 289–306. In: Marzluff, J.M., Bowman, R. and Donnelly, R. (Eds). *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA, USA.

Seress, G., Lipovits, Á., Bókony, V. and Czúni, L. (2014) Quantifying the urban gradient: A practical method for broad measurements. *Landsc. Urban Plan.*, **131**, 42–50.

Smith, J.A., Harrison, T.J.E., Martin, G.R. and Reynolds, S.J. (2013) Feathering the nest: food supplementation influences nest construction by Blue (*Cyanistes caeruleus*) and Great Tits (*Parus major*). *Avian Biol. Res.*, **6**, 18–25.

Stanley, T.R. (2002) How many kilojoules does a Black-billed Magpie nest cost? *J. Field Ornithol.*, **73**, 292–297.

404 Suárez-Rodríguez, M., López-Rull, I. and Garcia, C.M. (2012) Incorporation of cigarette butts into
405 nests reduces nest ectoparasite load in urban birds: new ingredients for an old recipe? *Biol.*
406 *Lett.*, **9**, 20120931.
407 Surgey, J., du Feu, C.R. and Deeming, D.C. (2012) Opportunistic use of a wool-like artificial material
408 as lining of tit (Paridae) nests. *Condor*, **114**, 385–392.
409 Tauber, M.J., Tauber, C.A. and Masaki, S. (1986) *Seasonal adaptations of insects*. Oxford Univ.
410 Press, Oxford, UK.
411 Tremblay, I., Thomas, D.W., Lambrechts, M.M., Blondel, J. and Perret, P. (2003) Variation in Blue
412 Tit breeding performance across gradients in habitat richness. *Ecology*, **84**, 3033–3043.
413 United Nations, Department of Economic and Social Affairs, Population Division (2014) *World*
414 *urbanization prospects: The 2014 revision, highlights (ST/ESA/SER.A/352)*. The United
415 Nations, New York, NY, USA.
416 Wesołowski, T. (2011) Reports from nestbox studies: a review of inadequacies. *Acta Ornithol.*, **46**,
417 13–17.
418 Wesołowski, T. and Stańska, M (2001) High ectoparasite loads in hole-nesting birds: a nestbox bias?
419 *J. Avian Biol.*, **32**, 281–285.
420 Wilkin, T.A., Gosler, A.G., Garant, D., Reynolds, S.J. and Sheldon, B.C. (2009) Calcium effects on
421 life-history traits in a wild population of the Great Tit (*Parus major*): analysis of long-term data
422 at several spatial scales. *Oecologia*, **159**, 463–472.
423 Winkler, D.W. (1993) Use and importance of feathers as nest lining in Tree Swallows (*Tachycineta*
424 *bicolor*). *Auk*, **110**, 29–36.

425 **Figure titles**

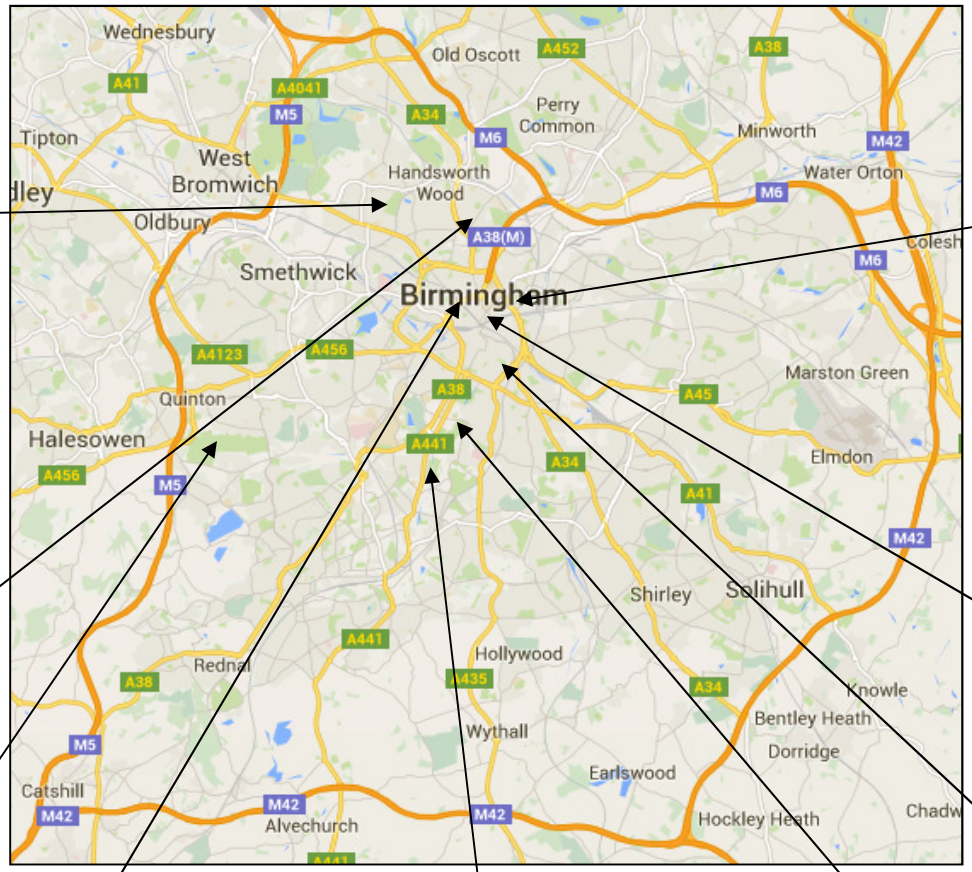
426 **Figure 1** The distribution of nine of the 31 sites in the city of Birmingham from which Blue Tit nests
427 were obtained from 10 nestboxes at each to investigate the effects of the degree of urbanisation on
428 their composition and ectoparasite load. See Appendix 1 for further details of how the urbanisation
429 measures were derived and of the 31 sites that were studied during 2014.

430 **Figure 2** The composition of Blue Tit nests collected from nestboxes at 30 sites in the city of
431 Birmingham in 2014 from various parts of the urban gradient categorised as low (0-33%), medium
432 (34-66%) and high (67-100%) according to (a) connected tree cover and (b) built cover (see Appendix
433 1 for further details of how urban measures were derived). Nest components are expressed as
434 percentages of nest mass (to control for differences in nest size) and Ns denote the number of nests
435 that were deconstructed for each category.

436 **Figure 3** Mean percentage mass of (a & b) feathers and (c & d) natural fibres in Blue Tit nests at 30
437 sites in the city of Birmingham in 2014 collected from nestboxes at various parts of the urban gradient
438 defined according to connected tree cover and built cover, respectively (see Appendix 1 for further
439 details of how urban measures were defined).

440 **Figure 4** The relationship between the mean ectoparasite load and the mean mass of nests of Blue Tits
441 containing chicks collected from nestboxes in the city of Birmingham in 2014 at various parts of the
442 urban gradient (see Appendix 1 for further details).


Handsworth


Wednesbury
Old Oscott
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A38
A41
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Tipton
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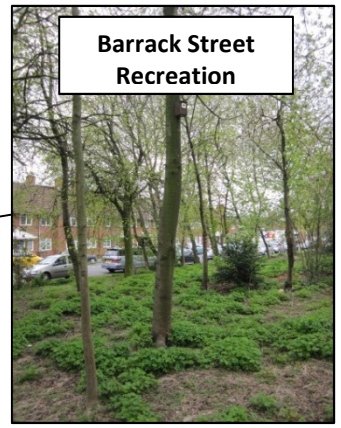
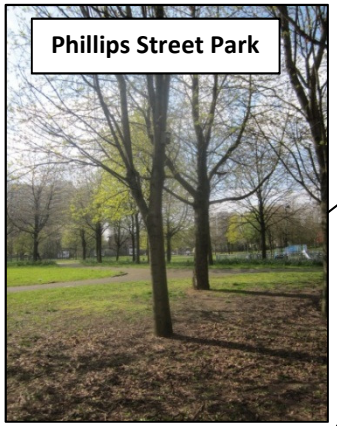
Minworth
M42
West Bromwich
Handsworth Wood
Water Orton
M6
Oldbury
A38(M)
M6
Smethwick
Birmingham
A4123
A456
Marston Green
A38
A45
Quinton
Halesowen
A441
A34
Elmdon
A456
M5
A41
M42
Shirley
Solihull
A441
Hollywood
Redn
A38
M42
A34
Knowle
Bentley Heath
Wythall
M5
Dorridge
Earlswood
Catshill
M42
M42
Alvechurch
M42
Hockley Heath


Barrack Street Recreation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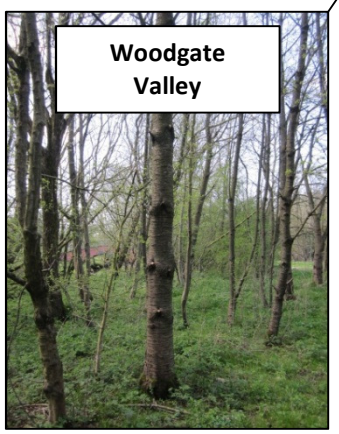
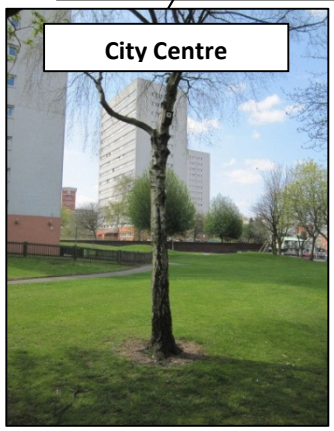
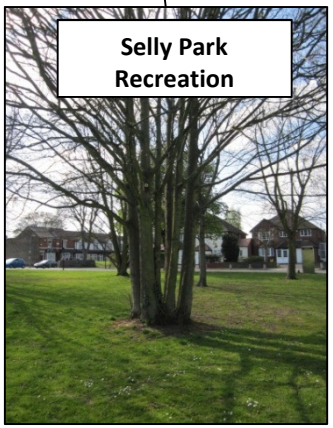
Park Street

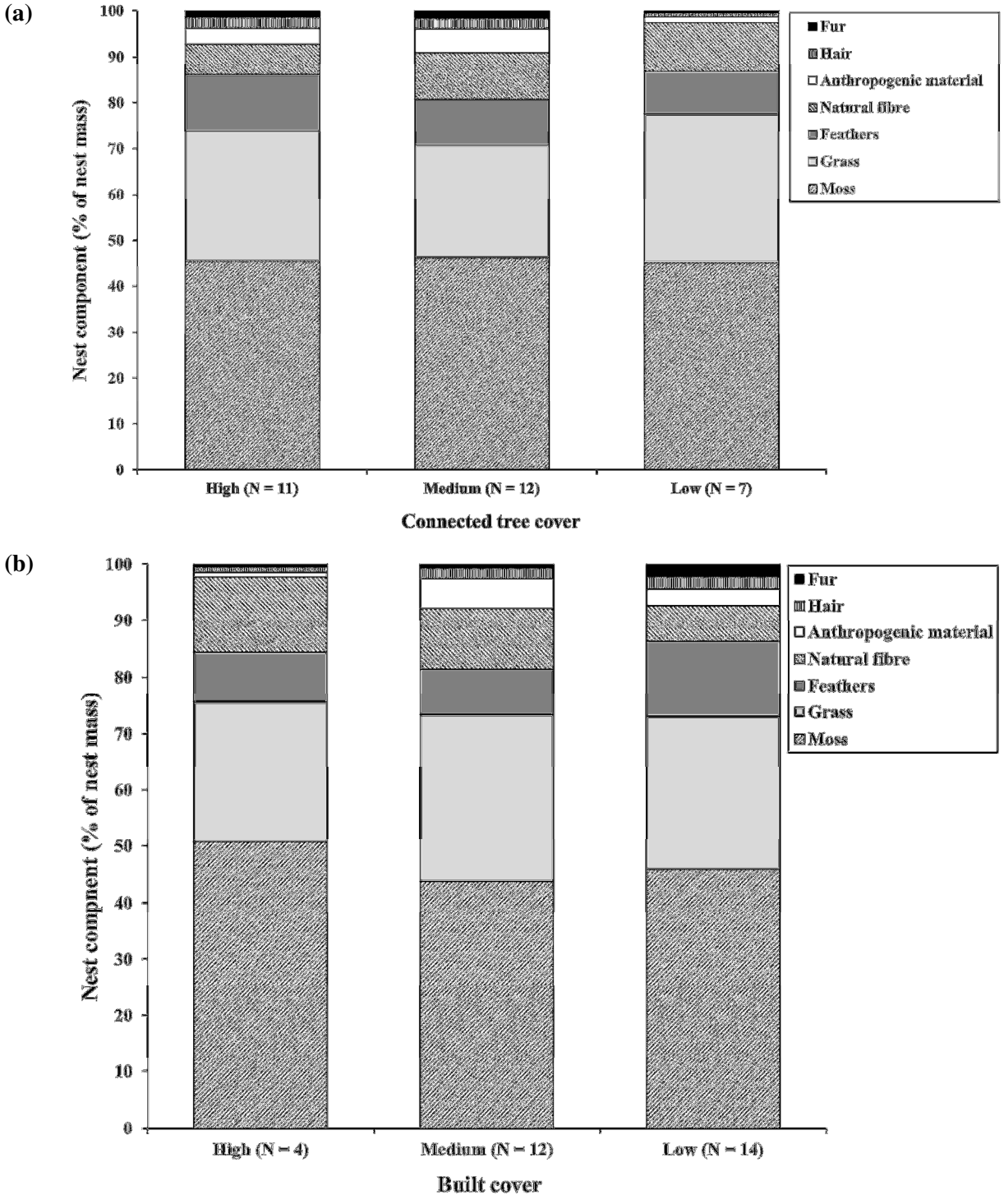

Woodgate Valley


City Centre

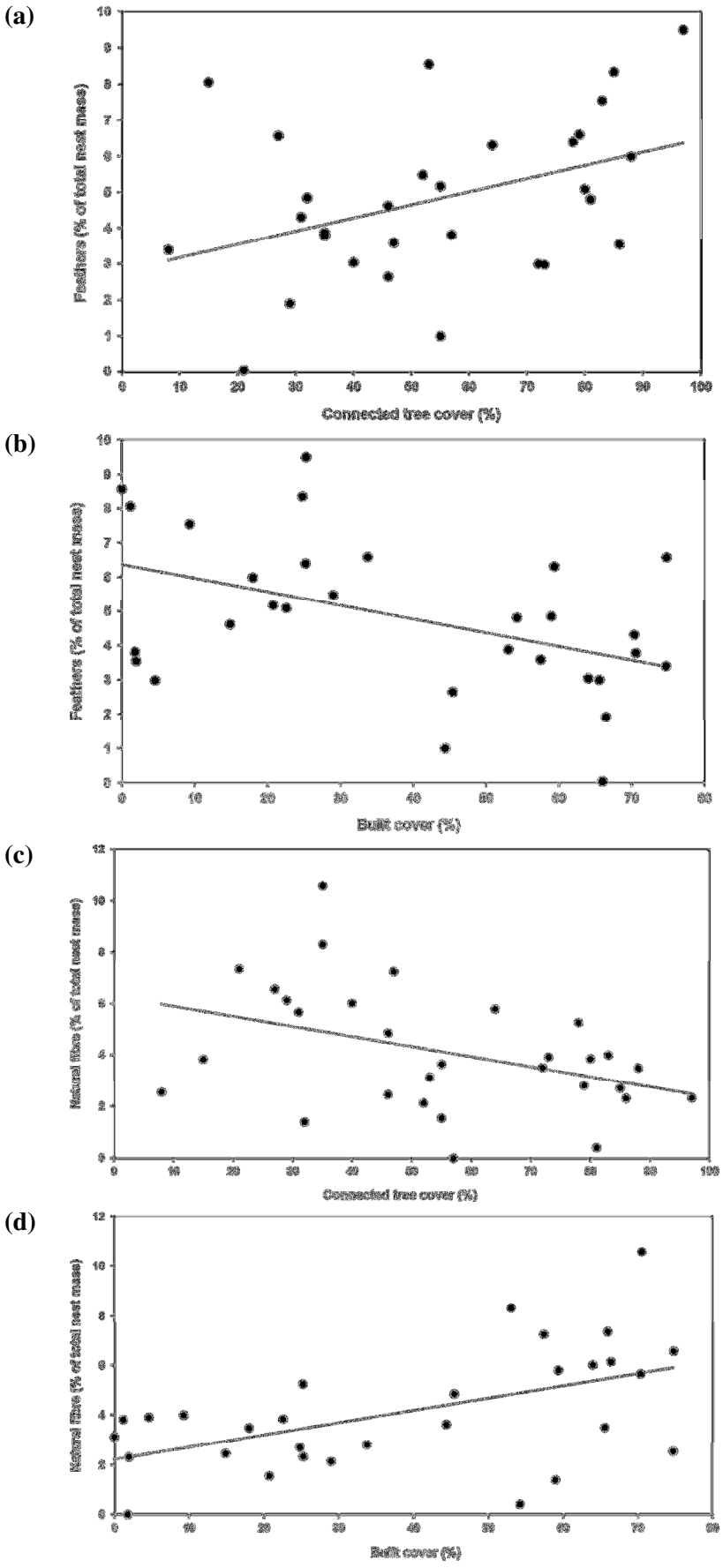

Selly Park Recreation


Cannon Hill Park

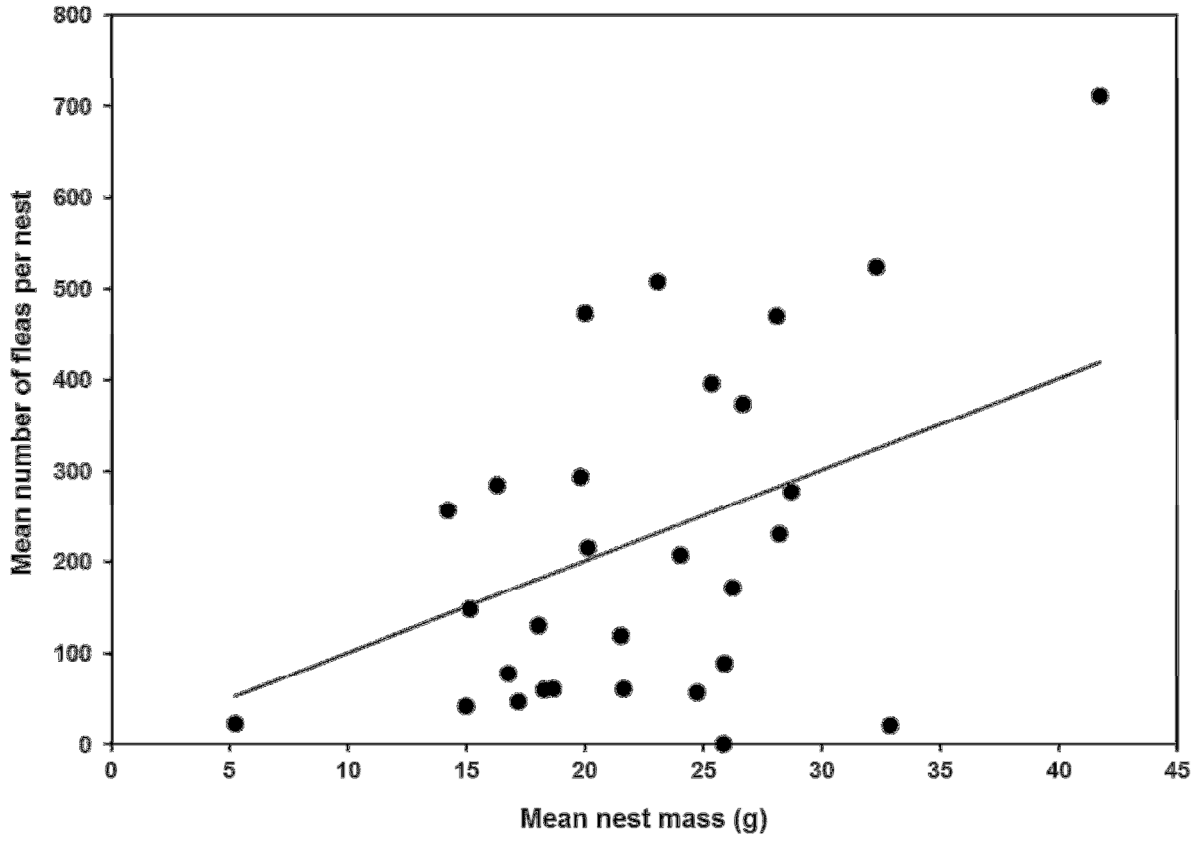

Highgate Park


(a)
Nest component (% of nest mass)
100
90
80
70
60
50
40
30
20
10
0
High (N = 11)
Medium (N = 12)
Low (N = 7)
Connected tree cover
Fur
Hair
Anthropogenic material
Natural fibre
Feathers
Grass
Moss
(b)
Nest compnent (% of nest mass)
High (N = 4)
Medium (N = 12)
Low (N = 14)
Built cover

444 **Figure 2.**


(a)
Feathers (% of total nest mass)
Connected tree cover (%)
(b)
Feathers (% of total nest mass)
Built cover (%)
(c)
Natural fibre (% of total nest mass)
Connected tree cover (%)
(d)
Natural fibre (% of total nest mass)
Built cover (%)

445 **Figure 3.**



446

447 **Figure 4.**

Appendix 1. Details of each of 31 nest sites along the urban gradient of the city of Birmingham, UK, from which Blue Tit nests were removed from nestboxes for deconstruction at the end of the 2014 breeding season.

Nest site location	Longitude	Latitude	Connected tree cover* (%)	Built cover* (%)
Barrack Street Recreation Ground	52.48712	-1.87998	64	59
Batchelors Farm Park	52.48228	-1.81945	46	15
Burberry Brickworks	52.45	-1.85503	46	45
Callow Brook	52.39754	-2.00746	72	66
Chamberlain Gardens	52.4741	-1.92784	81	54
City Centre Gardens	52.48058	-1.90888	27	75
Cowley Road Recreation Ground	52.45492	-1.85157	29	66
Garrison Lane Park	52.47975	-1.87418	21	66
Grand Union Canal	52.4799	-1.88319	27	81
Handsworth Park	52.51017	-1.92668	80	23
Highgate Park	52.46958	-1.88354	40	64
Hilltop and Manwood Country Park	52.51944	-1.94563	53	0
Holders Lane Woods	52.44227	-1.90883	83	9
Moillet Street Park	52.48831	-1.94518	32	59
Oakwood Road Coppice	52.54695	-1.84722	97	25
Park Lane Pos	52.52434	-1.79095	35	53
Park Street Gardens	52.48056	-1.88966	8	75
Perry Hall Playing Fields	52.52467	-1.91674	15	1
Phillips Street Park	52.49774	-1.89448	35	71
Popes Lane	52.41084	-1.95138	85	25
Rookery Park	52.51784	-1.8368	79	34
RSPB Sandwell Valley	52.53356	-1.95051	73	5
RSPB Woodland – Cannon Hill Park	52.44854	-1.90335	88	18
Selly Park Recreation Ground	52.4385	-1.92525	52	29
Sheldon Country Park	52.45663	-1.78889	78	25
Soho Pool Wharf	52.49608	-1.92231	55	44

Sutton Park	52.55792	-1.84301	57	2
The Radleys	52.46763	-1.77304	47	57
Warstone Lane Cemetery	52.4885	-1.91525	31	70
Woodgate Valley – Country Park	52.44891	-1.99576	86	2
Woodgate Valley – The Pines	52.43688	-2.0141	55	21

*Urban land cover measures were derived using GIS layers using Lidar vector data for connected tree cover and 2 × 2 m raster pixels for built cover. For both measures we know that a circle with a 250 m radius has a total area of 196,350 m^2 and this was used to calculate the number of 4 m^2 pixels (see above) that were built/unbuilt from the raster layer, and the area of connected tree cover from the vector layer. Both cover measures are then expressed as percentages of total areas at each site. For more general information regarding how such land cover measures are derived using GIS please see Hale *et al*. (2013).

Appendix 2. Details of the composition of Blue Tit nests removed from 30 nest site locations along the urban gradient of the city of Birmingham, UK at the end of the 2014 breeding season.

Nest site location	Mean nest mass* (± 1 SE) (g)	Mean nest dry mass (± 1 SE) (g)	Mean mass (± 1 SE) (g) at each nest site location of following nest components:						
			Moss	Grass	Feathers	Hair	Fur	Natural fibres	Anthropogenic materials
Barrack Street Recreation Ground	20.26 ± 4.07	8.90 ± 2.27	2.78 ± 1.20	1.90 ± 0.45	1.13 ± 0.39	0.18 ± 0.06	0.01 ± 0.004	0.99 ± 0.34	1.92 ± 1.80
Batchelors Farm Park	20.59 ± 3.45	8.70 ± 1.14	5.61 ± 0.94	1.62 ± 0.39	0.79 ± 0.20	0.03 ± 0.01	0.18 ± 0.10	0.35 ± 0.18	0.12 ± 0.11
Burberry Brickworks	26.22 ± 10.80	15.01 ± 6.11	10.04 ± 6.78	3.05 ± 0.69	0.67 ± 0.25	0.24 ± 0.21	0.03 ± 0.03	0.94 ± 0.43	0.05 ± 0.04
Callow Brook	19.68 ± 1.76	9.63 ± 0.88	6.03 ± 0.70	2.09 ± 0.22	0.58 ± 0.16	0.02 ± 0.007	0.01 ± 0.008	0.74 ± 0.30	0.15 ± 0.12
Chamberlain Gardens	18.88 ± 4.17	9.43 ± 1.44	4.29 ± 1.44	3.83 ± 0.23	0.91 ± 0.24	0.28 ± 0.09	-	0.09 ± 0.08	0.02 ± 0.01
City Centre Gardens	15.30 ± 3.01	8.92 ± 2.07	3.47 ± 1.11	3.07 ± 0.99	0.83 ± 0.21	0.17 ± 0.10	0.10 ± 0.04	1.14 ± 0.50	0.15 ± 0.06
Cowley Road Recreation Ground	24.02 ± 7.58	8.41 ± 0.82	3.90 ± 0.78	2.87 ± 0.30	0.41 ± 0.15	0.03 ± 0.01	0.02 ± 0.02	1.02 ± 0.57	0.18 ± 0.10
Garrison Lane	25.85	10.99	3.60	5.29	0.01	0.08	-	1.90	0.13

Park									
Handsworth Park	24.47 ± 2.51	7.58 ± 1.26	0.92 ± 0.44	3.50 ± 0.68	1.22 ± 0.13	0.06 ± 0.04	0.07 ± 0.06	0.92 ± 0.44	0.89 ± 0.56
Highgate Park	17.19 ± 3.14	7.88 ± 1.46	4.86 ± 0.90	0.84 ± 0.36	0.47 ± 0.16	0.27 ± 0.19	0.20 ± 0.16	1.18 ± 0.65	0.06 ± 0.04
Hilltop and Manwood Country Park	20.70 ± 2.75	9.62 ± 1.57	3.18 ± 0.67	3.85 ± 0.62	1.88 ± 0.62	0.03 ± 0.01	0.01 ± 0.01	0.66 ± 0.23	0.01 ± 0.007
Holders Lane Woods	18.26 ± 1.39	10.20 ± 0.53	5.11 ± 0.70	2.11 ± 0.61	1.37 ± 0.33	0.22 ± 0.11	0.09 ± 0.07	0.66 ± 0.21	0.64 ± 0.50
Moillet Street Park	23.00 ± 5.72	8.34 ± 1.53	4.05 ± 0.98	2.47 ± 0.13	1.22 ± 0.70	0.15 ± 0.02	0.01 ± 0.01	0.33 ± 0.13	0.11 ± 0.11
Oakwood Road Coppice	18.26	10.39	2.33	5.77	1.73	0.05	0.04	0.42	0.04
Park Lane Pos	15.78 ± 2.51	6.80 ± 1.07	2.03 ± 0.60	2.04 ± 0.48	0.64 ± 0.15	0.22 ± 0.12	0.14 ± 0.05	1.20 ± 0.31	0.54 ± 0.46
Park Street Gardens	19.36	8.96	4.90	2.85	0.66	0.02	0.01	0.49	0.03
Perry Hall Playing Fields	17.49 ± 1.47	8.71 ± 0.82	3.30 ± 0.63	3.13 ± 0.30	1.34 ± 0.45	0.06 ± 0.02	0.11 ± 0.09	0.71 ± 0.26	0.07 ± 0.05
Phillips Street Park	12.03 ± 2.95	7.10 ± 1.47	3.70 ± 0.70	1.35 ± 0.92	0.48 ± 0.23	0.08 ± 0.02	0.02 ± 0.01	1.43 ± 0.95	0.03 ± 0.03
Popes Lane	17.42 ± 1.35	7.49 ± 0.48	4.30 ± 0.65	1.25 ± 0.34	1.38 ± 0.24	0.13 ± 0.05	0.01 ± 0.003	0.43 ± 0.17	0.01 ± 0.004
Rookery Park	26.66 ± 2.08	9.39 ± 1.34	2.74 ± 0.85	3.77 ± 0.56	1.70 ± 0.41	0.20 ± 0.09	0.06 ± 0.04	0.73 ± 0.23	0.19 ± 0.12
RSPB Sandwell Valley	17.88 ± 3.81	8.24 ± 1.29	4.94 ± 0.74	1.20 ± 0.36	0.45 ± 0.19	1.08 ± 0.81	0.02 ± 0.01	0.55 ± 0.30	0.005 ± 0.004

RSPB Woodland – Cannon Hill Park	18.81 ± 2.19	11.19 ± 3.29	5.30 ± 1.47	1.93 ± 0.59	1.01 ± 0.35	0.01 ± 0.01	0.98 ± 0.98	0.51 ± 0.32	1.45 ± 1.24
Selly Park Recreation Ground	26.23 ± 7.90	10.85 ± 5.05	2.17 ± 0.38	4.77 ± 3.88	1.63 ± 0.86	0.79 ± 0.31	0.39 ± 0.11	0.89 ± 0.89	0.21 ± 0.12
Sheldon Country Park	24.09 ± 6.32	8.42 ± 1.38	3.72 ± 1.04	2.19 ± 0.30	1.30 ± 0.33	0.04 ± 0.01	0.02 ± 0.02	1.08 ± 0.54	0.07 ± 0.05
Soho Pool Wharf	15.91 ± 3.89	6.95 ± 1.65	2.29 ± 0.59	2.18 ± 1.16	0.13 ± 0.07	0.12 ± 0.05	-	0.66 ± 0.32	1.57 ± 1.51
Sutton Park	20.70	8.70	5.22	1.10	1.37	0.16	0.66	-	0.20
The Radleys	25.43 ± 4.41	10.68 ± 1.80	4.02 ± 1.33	2.96 ± 0.79	0.99 ± 0.33	0.36 ± 0.24	0.07 ± 0.07	2.07 ± 1.16	0.22 ± 0.17
Warstone Lane Cemetery	18.63 ± 4.81	7.30 ± 1.90	4.16 ± 1.27	1.03 ± 0.37	0.87 ± 0.55	0.03 ± 0.02	0.02 ± 0.02	1.12 ± 0.36	0.07 ± 0.02
Woodgate Valley – Country Park	22.20 ± 3.23	10.83 ± 1.47	7.54 ± 1.67	1.35 ± 0.38	0.77 ± 0.19	0.22 ± 0.13	0.36 ± 0.35	0.49 ± 0.20	0.10 ± 0.09
Woodgate Valley – The Pines	26.85 ± 6.98	12.54 ± 2.63	8.08 ± 2.22	2.36 ± 0.64	1.28 ± 0.24	0.10 ± 0.06	0.02 ± 0.02	0.50 ± 0.27	0.19 ± 0.18

*Nests weighed immediately after their removal from the chest freezer but before thawing and deconstruction – see Methods for further details. '-' signifies an absence of a nest component.